THE ALIMENTARY CANAL AND PANCREAS OF *ACIPENSER, AMIA*, AND *LEPIDOSTEUS*.

By A. B. MACALLUM, B.A., *Fellow of University College, Toronto, Canada.* (PLATE XX.)

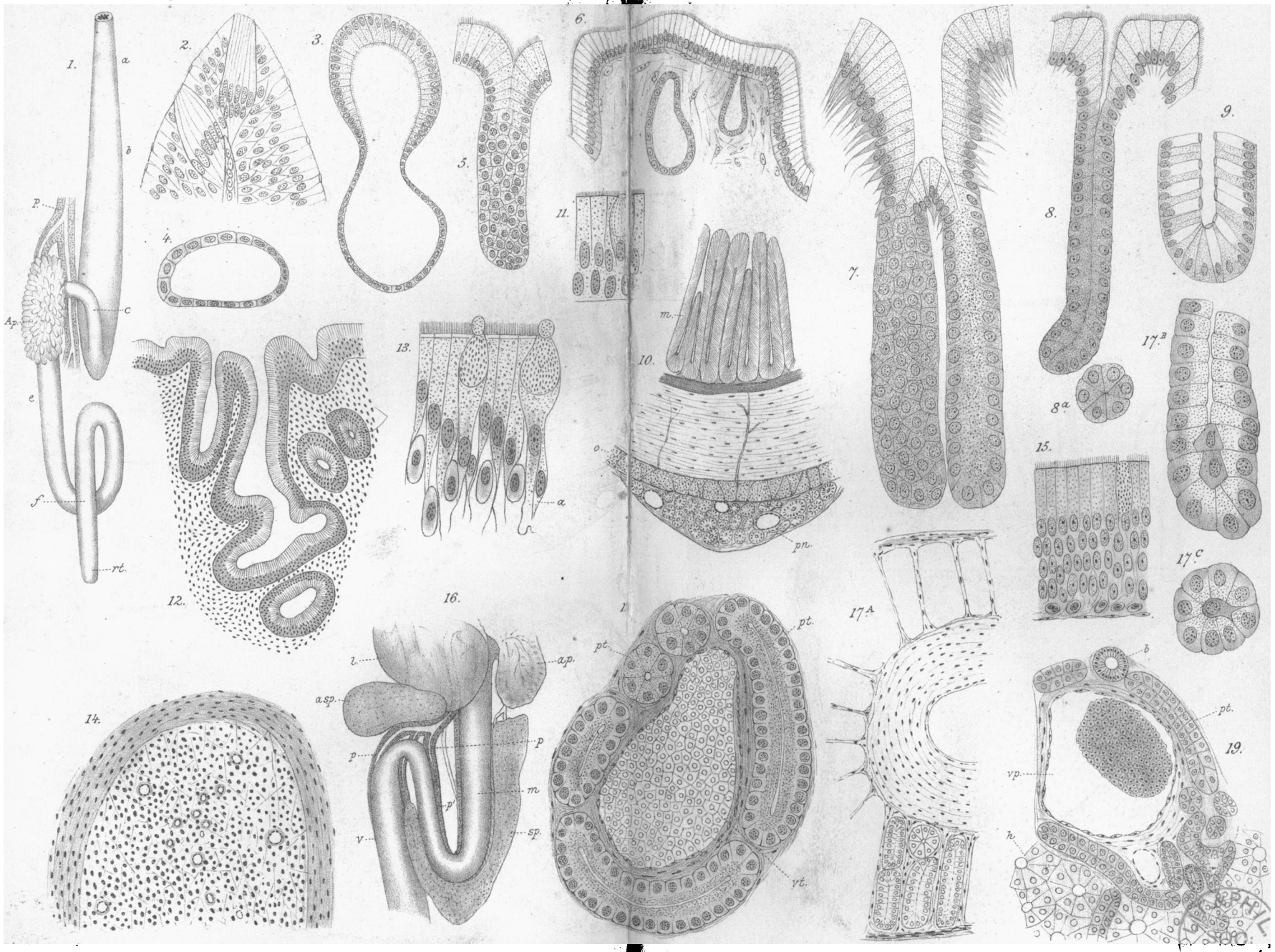
THE investigation, some results of which appear in the present work, was begun two years ago, with the object of treating fully of the digestive organs of fishes in general. Since I have now had for some time but few opportunities for continuing the research further, and do not expect to be more fortunate in this respect for a year or so to come, I have been led to abandon that object wholly. The results of my studies, however, so far as they relate to Ganoid fishes, seem to me to have some value, and I have therefore decided to publish them.

The description here given, so far as it pertains to *Lepidosteus*, is based on forms of 7–10 cm. in length, which I was forced to accept for the purpose, since the adult forms are to be obtained from remote places only, and always in a poor state of preservation for histological examination. As a full description of the histology of the intestinal tract in young *Lepidostei* would not correspond in every respect to the conditions obtaining in the adult forms, I have endeavoured to omit references to peculiarities of structure such as may be affected by age.

The terms fore-gut, mid-gut, and hind-gut are here employed for the purpose of description, as they answer to the conditions of the alimentary canal in fishes better than any others that can be suggested. They have already, to a certain extent, been sanctioned by usage, since they are employed in the English edition of Gegenbaur's *Elements of Comparative Anatomy*.

FORE-GUT.

Œsophagus.—In *Acipenser*, that part of the alimentary canal lying behind the branchial chamber, and terminating about 3 cm. behind the membrane separating the pericardial and peritoneal cavities, is usually considered to be the œsophagus. It is comparatively short, and is at once recognisable by the large number of papillæ arranged in longitudinal series on its inner surface.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In its wall are found the two layers of striated muscular fibre, commonly present in the œsophagus of fishes.

There are, however, elements in the structure of this part of the alimentary canal which throw some doubt on its being homologous with the œsophagus of other vertebrates. It is lined with an epithelium formed of many layers of fusiform, polyhedral, or flattened cells, which do not differ to any appreciable extent from those of the membrane lining the posterior part of the pharyngeal chamber. This kind of epithelium is rare in the œsophagus of fishes.[1] There are also to be found in this part taste-buds, occurring usually on the summits of the papillæ already referred to. I have never seen any reference to the occurrence of such structures in the œsophagus of any vertebrate,[2] but they are to be met with commonly in pharynx, especially in fishes. That part of the fore-gut in *Acipenser* immediately following the so-called œsophagus is devoid of striated muscle, and therefore might be regarded as part of the stomach. But this is not a sure method of distinguishing the two divisions of the fore-gut, for if the anterior part possesses glands which secrete a digesting principle, the absence of voluntary muscular fibre is a necessary condition, in order to allow the secretion to perform its function. The anterior part of the fore-gut in *Acipenser* does possess glands of this description, hence the absence of striated muscular fibre from its wall. It will be seen farther on, that the division of the fore-gut into œsophagus and stomach is not very marked in *Amia* and *Lepidosteus*, the passage from one to the other part being at best but a gradual one. That part following the papillated section of the canal in *Acipenser* must be regarded, therefore, as the true œsophagus, and from its structure, as described below, it may be correctly said to terminate a short distance behind the opening of the duct of the air-bladder, near the commencement of the gastric loop.

The papillated portion is then but the posterior extension of the pharynx. Its inner surface is greyish-white, and the few

[1] According to Edinger (*Arch. für Mikr. Anat.*, Bd. xiii. p. 651) a several-layered scale-like epithelium is present in the œsophagus of *Polypterus* and of some Selachians.

[2] In *Amphioxus* I have, however, determined the presence of taste-buds as far posteriorly in the alimentary canal as the opening of the "hepatic" cæcum.

folds that are present run longitudinally between the series of papillæ. It terminates about 3 cm. behind the pericardial chamber. The epithelium lining it is constituted of from five to ten layers of cells, which are usually fusiform, often polyhedral or squamous, the superficial layer being, however, formed of cylinder and goblet cells almost invariably. F. E. Schulze[1] found the cylinder cells provided with cilia. I am unable to confirm this, although I have studied the epithelium in fresh and in hardened condition. The theca of each goblet cell is of an elongated oval shape and is filled with mucus, containing a large number of feebly refracting granules. Many of the cylinder cells also exhibit a mucigenous transformation of their contents. The basal processes of both forms of cells are exceedingly fine and delicate. The replacement of the cast-off goblet cells, into which all the cylinder cells are metamorphosed, is accomplished by those of the layer next below them.

The taste-buds are not different from those found in the mouth, except perhaps in their slightly more elongated form (fig. 2). Several may be found on the summit of a papilla.

The true œsophagus possesses to the naked eye all the characteristics of the stomach. The colour of its lining membrane is, in the fresh condition, chocolate-red, and its folds pass uninterruptedly, without increase or decrease in size into, those of the stomach. The calibre of both parts of the fore-gut is the same. The only distinctions to be found between them lie in the histological structure of the mucosa. The point of transition between the œsophagus and stomach, as already stated, is near the gastric loop, up to which point the epithelium of the former retains its cilia, while the peptic tubules found in it are somewhat different from those of the loop.

In *Amia* the œsophagus is short, and terminates immediately behind the opening of the duct of the air-bladder. As in *Acipenser*, the inner surfaces of both œsophagus and stomach are alike in every respect when viewed with the naked eye. The folds in both parts are continuous and arranged longitudinally, while the dull reddish tint of the mucosa of the stomach is possessed to some extent by that of the œsophagus. Where one part ends and the other begins can be determined approximately

[1] *Arch. für Mikr. Anat.*, Bd. iii. p. 174.

only, the lining epithelium and the glands of the anterior part passing without any abrupt change into those of the posterior. Taking the presence of striated muscular fibre as a guide in this determination, although a very uncertain one, the two parts may be divided as œsophagus and stomach at the point intimated.

In *Lepidosteus* the œsophagus commences immediately anterior to the opening of the air-duct; where it terminates posteriorly it is difficult to say. The distinction between the two parts of the fore-gut is not less indefinite, perhaps more so, than in the other two genera. For a third of the extent of the straight tube forming the fore-gut, the epithelium in character and the glands in both character and number differ considerably from the corresponding structures in the posterior two-thirds, although, so far as the glands are concerned, the transition from one to the other part is a gradual, not an abrupt one. The anterior third, which may therefore be termed the œsophagus, does not seem to have any striated muscular fibre in its outer wall, but the specimens from which my preparations were taken were not of such an age as to allow me to speak with certainty on this point.

The opening of the air-duct in *Amia* and *Lepidosteus* is a longitudinal slit on the dorsal side of the œsophagus. This opening is provided with two folds, one on the right, the other on the left, which can be approximated by the striated muscular fibre present in them to shut off, after the fashion of a glottis, all connection between the duct and the cavity of the œsophagus. The muscular fibre is very abundant in *Amia*, in which it radiates out over the duct and on the surface of the air-bladder. In *Acipenser*, in which the opening of the duct is funnel-shaped, there is apparently no mechanism by which the cavity of the air-bladder can be completely closed off from that of the œsophagus.

In *Acipenser*, *Amia*, and *Lepidosteus* the epithelium of the œsophagus is ciliated. The cilia in the first named form a thick brush on each cell, and all usually matted together by mucus; in the other two genera they are much longer and finer. The cells in all are cylindrical, with fine basal processes which pass into and are interwoven with the connective tissue of the mucosa. In *Acipenser*, in the outer or peripheral halves of a large number of these cells, the contents are swollen like those

of the goblet cells, but the staining with various dyes is uniform in the inner and outer cellular portions, the absence of mucigen being thereby shown. In *Amia* many of the cells have lost their cilia and are changed into goblet cells; this is more commonly the case in the shallow crypts which are to be found abundantly over the mucous surface. All the cells exhibit the mucigenous transformation. In *Lepidosteus* the cells are of regular form, with their outer portions containing a quantity of mucigen. Cilia were observed on all the cells. In this genus, as well as in *Acipenser*, some of the cellular elements must, before they break up or are destroyed, open peripherally to discharge their mucus.

In the opening of the air-duct in the three genera the cylinder cells are short, and in the middle of the extent of the duct they become cubical. In *Lepidosteus* the folds at the side of the opening are covered with short columnar cells.

In *Acipenser* and *Lepidosteus* the derivatives of the epithelium in the œsophagus may be referred to three forms:—(1) elongated crypt-like insinkings; (2) elongated crypts terminated in dilated sacs; (3) true gland tubules. In *Amia* in addition to these three classes of structures there is a fourth, examples of which are to be found in the neighbourhood of the mouth of the air-duct, in the latter and even in the air-bladder.

The elongated crypt-like insinkings of the epithelium are apparently most common in *Acipenser* in which they are specially noticeable at the commencement of the œsophagus. They are not always straight in their course through the mucosa. The ordinary epithelium of the general surface is continued into them for half their length, while the lower half of the cylinder cells, though still retained, are shortened, much so in *Amia*, and their cilia less prominent. In these the nuclei are placed next the membrane of connective tissue surrounding the crypt; the contents of the central portions of the cells appear to be mucigenous when viewed in sections of the hardened tissue, but when observed after isolation in serum the mucigen is obscured by the presence of fatty matter in the form of minute globules, which are more abundant near the lumen. In *Amia* the corresponding cells are shorter and the central half of each is packed full of granules, whether of

zymogen or not I am unable to say. In *Lepidosteus* these insinkings of the epithelium are found only at the posterior end of the first third of the fore-gut, and their cells are much shortened, often reaching a cubical form.

In *Acipenser* these crypts may branch more than once, although as a rule they do not branch at all. In this genus they are not found farther than 2 cm. behind the commencement of the œsophagus, where they become changed into the structures of the third class mentioned above. This change is a gradual one, the cells at the bases of the crypts, as the latter are followed backward, becoming shorter and more cubical, assuming at the same time a more specialized glandular character. In *Amia* also, these insinkings are least numerous where the true gland tubules are most so, and passage-forms between the two classes of structures are present.

Elongated crypts terminating in dilated sacs are not numerous in *Acipenser*, and *Lepidosteus* and in *Amia*, in which they appear to occur in the largest number, they bear a very small proportion to the structures of the first class. As to their character they are most highly developed in *Acipenser* and least so in *Lepidosteus*. The tubular part is lined with cylinder cells which decrease in length as the sac is approached, while the cilia become shorter and less abundant. There is in *Acipenser* a slight constriction of the tubule where it terminates in the sac; at this point the cilia vanish and the cells attain their greatest decrease in height. The cells lining the sac and their nuclei are flattened, but the form never becomes squamous. What little protoplasm there is surrounding the nuclei appears clear and transparent.

Sometimes in *Amia* one or more gland tubules are found to open into one of these sacs. This is the case in young forms particularly. I have not, however, observed a like arrangement in the two other genera, but whether it occurs in them or not these sacs are still remarkable on account of their structure, since they have not, as far as I am aware, been observed in any other fish. Their fewness of number and their limited distribution in *Acipenser* also render them worthy of note. They cannot serve in any case for the purpose of absorption, since they are placed too far in front of the seat of digestive changes,

and as they are undoubtedly devoid of a glandular function, one is compelled to consider them to be transudatory organs. A careful study of the histology of the fore-gut in a large number of fishes may show the presence of these structures to be more general.

True gland tubules are most abundant in the œsophagus of *Acipenser* and fewest in *Lepidosteus;* in the latter they are only to be found at the posterior end of the œsophagus. In the first named genus they are usually much elongated, the elongation increasing as they are followed backward. Large cubical cells line them and enclose a lumen of considerable size. The contents of the central half of each cell stain with difficulty in carmine, while the contrary is the case with the outer half in which the nucleus is placed. The edge of the cell touching on the lumen is very irregular and ragged in appearance, owing to the abundance of granules present.

The neck of each tubule and the crypt into which it opens constitute from one-third to one-half the length of the three parts, and in this respect there is a marked contrast to the glands of the anterior portion of the stomach in *Acipenser*, or to those in any part of the cardia in the other genera. In the crypt the epithelium is the same as that of the general surface, being ciliated and cylindrical. In the neck of the gland the cells are transitional in their form, and contents between those of the crypt and those of the body of the tubule, being nearly cubical in form, and containing a non-granular protoplasm with a narrow zone of mucigenous matter in each, which borders on the lumen.

There is in *Amia*, as already mentioned, a fourth variety of tubules occurring at the mouth of the air-duct, and appearing to be similar in every respect to that found in the air-duct itself, and on the inner surface of the inferior wall of the air-bladder. Tubules of this sort are not numerous. They and the crypts into which they open are very short. Their cells are narrower and shorter than those of the other kinds of tubules described. Sometimes the contents of the cells are strongly granular, at other times they are constituted of mucus almost wholly. The lumen of the tubule is more frequently indistinct.

I had not, unfortunately, an opportunity of studying these

tubules in a fresh condition, when a careful examination of them might reveal more about their function. They are in all probability but degraded forms of the true gland tubules of the œsophagus. A wider knowledge of the histology of the air-bladder in fishes may show that the occurrence of tubules of this description is not confined to *Amia*, since the air-bladder, before its function had become hydrostatic, probably acted as an accessory secreting organ provided with the same histological structure as the fore-gut from which it originated as an out-growth, and ought, therefore, still to have in many cases traces, though rudimentary, of this similarity.

Stomach.—The stomach in the three genera shows a considerable difference of form. The division of it into cardia and pylorus is easily distinguishable, much more so than is the division of the fore-gut into œsophagus and stomach.

In *Acipenser* the stomach is thrown into a loop which extends forward in front of the mouth of the air-duct, where the cardiac portion terminates in a retort-like pylorus. The wall of the cardia does not differ in thickness from that of the œsophagus, but in the pylorus the thickness is from one and a half centimetres, especially at the upper and under surfaces, at each of which the muscle fibre is collected into a thick plate-like mass; this in the relaxed condition of the pylorus lies flat on its fellow of the opposite side. At the right and left borders of these thickened plates the wall of the pylorus is as thin as in the cardia. In the latter the colour of the mucous membrane in its fresh condition is chocolate-red and the folds are arranged longitudinally, while in the pylorus the mucous membrane is dull white and its surface smooth. Viewed from without there is a contrast in the colour of the two parts of the stomach, that of the pylorus being a glistening white. In a sturgeon measuring 66 cm. the cardia was 16 cm., and the pylorus 3 cm. in length.

In *Amia* the cardia is dilated and its cavity is continued behind into a conical cæcum. The pyloric tube originates from the lower side of the cardia and passes forward and outward, undergoing a constriction where it unites with the mid-gut. The wall of the stomach is of equal thickness throughout, except for a slight increase of the muscular tissue

near the termination of the pylorus. The mucous membrane is folded, the direction of the folds being longitudinal; its colour is the same in the first half of the pylorus as it is in the cardia and cæcum. The surface of the membrane in the posterior half of the pylorus is nearly smooth. The colour here is a dull white.

In *Lepidosteus* the calibre of the stomach increases as it passes backward. Its cæcum, if it can be said to have any, is very short. Its mucous membrane is raised into longitudinal folds. On the inferior surface the narrow pyloric tube passes forward a short distance, then turns to the right, and terminates in the mid-gut immediately in front of the lobulated pyloric appendage.

The epithelium of the stomach in *Acipenser* is somewhat different in character from that in the œsophagus, and it differs even in the cardia and pylorus. The cells constituting it in the cardiac portion are longer and more slender than those in the œsophagus, and smaller than those in the pylorus They are unciliated, a peripheral membrane is present in each, and their contents do not apparently show any traces of that transformation into mucigen usually observable in the gastric epithelium of other vertebrates. The staining in my preparations is quite uniform throughout each cell. Only when Müller's fluid or a solution of potassic bichromate had been used as a hardening reagent did any of the cells, and then only a few, exhibit a peripheral opening. When alcohol alone had been used in preparing the epithelium the peripheral wall of each cell appears thick, probably owing to a deposit of mucus on the outside.

In the pylorus of *Acipenser* the majority of the cells of the epithelium are open peripherally; from this, and from their being sometimes swollen, they bear a resemblance to goblet cells. The contents of the distal half of each cell are almost completely mucigenous. A thick dense layer of mucus is often found to cover the epithelium, but it does not dip down into the crypts, although it accommodates itself to the general surface of the mucous membrane. Scattered throughout this layer of mucus a large quantity of granules together with nuclei of broken-down cells can be observed.

In *Amia* the epithelium is ciliated throughout the cardia,

cæcum, and pylorus. The cells are long and cylindrical, slightly swollen at their peripheral halves, and they are covered in chromic acid preparations by a thin coat of mucus. The contents in the peripheral half of each cell do not appear in fresh condition to differ from those in the central half, but when hardened and stained it is usual to find the outer half of the cell completely uncoloured. The cilia are obscured by the coat of mucus, but in the deeper crypts when this is absent they can be easily observed.

In *Lepidosteus* the epithelium of the posterior two-thirds of the fore-gut is unciliated, except in the posterior half of the pyloric tube. The cylinder cells are always provided with a peripheral membrane. They contain mucigen, as they are stainable only in their central halves.

The glands of the cardia in *Acipenser* are of the type to be usually found in fishes (fig. 7). The crypts of the epithelium, into which several gland tubules may open, have evidently been mistaken by Leydig[1] for glands, and they form, according to him, as such the only kind observable in *Acipenser*. Edinger,[2] commenting on Leydig's description, remarks that it is doubtful if *Acipenser* has true gastric glands, for the structures figured and described by Leydig bear no resemblance at all to the peptic glands of other fishes. Wiedersheim,[3] also misled by Leydig's description, doubts the existence of peptic glands in the Sturgeon. I am unable to explain how Leydig came to overlook the true glands, unless it is that in the species studied by him the epithelial crypts are actually the only approach to the form of glands present. This is not probable, however, and further attention given to the structure of the gastric mucosa in *A. nacarii* and *nasus*, the species employed by Leydig in his research, will in all likelihood show glands not differing to any appreciable extent from those observed by me in *A. rubicundus*.

The cells of the tubules may be classed according as they occupy the neck or the body of the gland. Those in the neck evidently do not secrete pepsin, as they lack granules and gene-

[1] *Untersuchungen über Fische und Reptilien*, Berlin, 1853, p. 16 ; also *Lehrbuch der Histologie*, 1857, p. 313.

[2] *Arch. für Mikr. Anat.*, Bd. xiii. p. 651.

[3] *Lehrbuch der Vergleichenden Anatomie der Wirbelthiere*, p. 581.

rally take a uniform stain with hematoxylin or carmine. They are transitional in their form and characters between the ordinary epithelial cells and those of the body of the tubule, being similar to the latter in size and shape. In this part of the gland the lumen is distinct in the body, usually it is not. The true gland cells are rhombohedral in shape; the nucleus in each is placed in the half of the cell removed from the lumen, and the contents of the central half are very granular and difficult to stain. In preparations made from a Sturgeon which had undergone previously a prolonged period of hunger, the staining which these cells took was more uniform. Ordinarily they are seen, when isolated, to have each a fine process, which, when the cell occupies its position in the tubule, is directed downwards between the membrana propria and the cell next below. These processes are to be observed in the gastric glands of many fishes, for example in *Perca*, *Amiurus*, *Gasterosteus*, *Stizostedion*, *Esox*, &c., and they seem to point out that the development of epithelial cells into gland cells is not a complete one in fishes, so far as form is concerned.

These glands are more numerous, but shorter near the pylorus. In the pylorus they are replaced by the less numerous mucous tubules, which are very much elongated, and provided each with a wide lumen (fig. 9). The cells constituting them are of two kinds: short goblet cells and columnar cells, the latter being sometimes wholly replaced by the former. The columnar cells are closed and their contents slightly granular. In the goblet cells the greater part of each is formed of a moderately swollen theca, the contents of which are clear, unstainable, and apparently formed of mucigen. The nuclei in both forms of cells are placed next the membrana propria of the tubule. These mucous glands are evenly distributed throughout the pylorus; the replacement of the cardiac glands by them is an abrupt, not a gradual one.

In *Amia* one or more gland tubules may open into each short crypt of the epithelium. As in *Acipenser* the cells of the neck and those of the body of the tubule are quite different. Those of the body are provided with fine processes also. The lumen is distinguishable usually only as a line in the axis of the tubule, but it is seen more clearly in transverse section (fig. 8). The gland cells are small and but slightly granular. Since all my

preparations were made from specimens of *Amia* which had gone without food for nearly two months, I am unable to speak of the condition of these cells during activity. As it is, they and their nuclei stain deeply and nearly uniformly. The cells of the neck are fewer in number compared with those of the body of the gland than in *Acipenser*. In the pylorus they become more numerous at the expense of the gland cells. About the middle of the extent of the pylorus the neck cells form about three-fourths of the tubule, while a few millimetres farther on the gland cells vanish completely. The tubules then in the posterior half of the pylorus are formed of cells, not differing from those in the necks of the cardiac glands except in the greater abundance of cilia.

In *Lepidosteus* the gland cells in the cardiac tubules are small, but their nuclei are large. Granules were not observed in the interior of the cells during either their resting period or their functional activity. Naturally a different result would be obtained in the case of a fully adult form. The cells stain uniformly in carmine or hematoxylin. Mucous glands, such as are figured by Edinger from the posterior part of the stomach, were not developed in the specimens from which my preparations were made. In the shallow cavity answering to a cæcum the few tubules present had a larger lumen than those in the main portion of the stomach, but are shorter in length.

THE MID-GUT.

The mid-gut in *Acipenser* has a different arrangement as regards its coils and loops from what it has in either *Amia* or *Lepidosteus*.

In *Acipenser* the anterior or duodenal portion is a straight tube of about 12 cm. length (in a specimen measuring 66 cm.), and terminates in a median portion of 7 cm., which is directed forward to pass into the posterior, or valvate section of the intestine. The latter portion, which tapers into the rectum or hind-gut, contains the spiral valve. The median part is as a rule of smaller calibre than the others, from which it is marked off by a slight constriction at each end. The valvate part is of largest diameter and provided with the thickest wall. It is supplied with a vein and an artery, both of considerable

size, which accompany the coils of the spiral valve about the axis of the intestine. The course of the two vessels appears usually very distinct through the muscular layers and the serosa, but sometimes the amount of pigment present is such as to obscure them. It is noticeable in the other portions of the intestine, as well as here, that pigment tissue is distributed chiefly along the course of the vascular channels. The valvate portion of the mid-gut measures about 20 cm. while the hind-gut is not more than 1 cm.; the former is also greater in length than the anterior and median sections taken together.

In *Amia* the anterior straight portion of the mid-gut measures 18 cm. (in a full grown specimen of 55 cm.), nearly occupying the length of the peritoneal cavity. It is connected on the left with a median portion of 9 cm., which is directed forward, and terminates opposite the cæcum of the stomach in the posterior part answering to the valvate section of the mid-gut in *Acipenser*, but having a very small portion of itself occupied by the spiral valve. The rectum or hind-gut does not measure more than 2 cm. The spiral valve is 3 cm. long, the total length of the mid-gut in front of it being 32 cm.

In figures of the intestine in *Amia* which have been given hitherto, the mid-gut is represented wrongly with a calibre greatly decreasing as it extends backward. The only decrease in size which occurs at all is to be found in the rectal portion.

In *Lepidosteus* there seems to be a great difference in the number and arrangement of the loops, according to the size of the specimen examined. In young forms it is as represented in fig. 1. Consulting, however, the figure of the intestines, as given by Balfour and Parker[1] in their work on the structure and development of *Lepidosteus*, one sees there a more complicated looping of the mid-gut, which, according to these authors, possesses three compact coils. The specimen of *Lepidosteus* from which their figure was drawn measured 100 cm. I was consequently at first of the opinion that the figure given here represents a very early condition, but such a condition is indicated by van der Hœven[2] in a case where the alimentary

[1] *Phil. Trans.*, 1882, pt. i. p. 359.

[2] "Ueber die zellige Schwimmblase des Lepidosteus," Müller's *Archiv*, 1841, and pl. x.

canal measured 30 cm., and, moreover, notes made three years ago, when I was dissecting a smaller specimen, seem to show that this arrangement persists for a large part of the life of the fish.

It is, however, not surprising that great differences should be found in the mid-gut of *Lepidosteus* and of fishes generally. I have elsewhere[1] called attention to the unequal growth of this part of the intestine in *Amiurus nigricans* during its life history. In this fish it was shown that the mid-gut of one of 60 cm. body-length measured more than treble that of a specimen of 38 cm. This disproportion in the growth of the mid-gut, in relation to the growth in length of the body, is noticeable in other fishes also. In consequence, the difference in the arrangement of the loops in the mid-gut in *Lepidosteus* is explained on the ground that an increase in size of the body calls for a greater increase in the length of the principal part of the absorptive tract, which is thereby thrown into a larger number of coils.

The arrangement of the loops in a young *Lepidosteus* is interesting on account of its similarity to that in the mid-gut of *Amia*. It appears probable then that this was the disposition of the parts in the mid-gut in both genera before the spiral valve had acquired its present rudimentary condition.

The pyloric valve in *Acipenser* and *Amia* takes the form of a tube projecting into the cavity of the mid-gut for a centimetre or more. A valve like this is present in *Lepidosteus*, according to Balfour and Parker; it is present in young forms of 7–10 cm. length, but it is not fully developed. In *Acipenser* and *Amia* it is provided with a thickened ingrowth of the fibre of the *muscularis mucosæ*.

The inner surface of the anterior, or duodenal section of the mid-gut in *Acipenser* is covered with a thick mucous membrane honey-combed with crypts of various size, the openings of the majority of which are very plainly visible. There is otherwise but little unevenness of surface. If the membrane is in a bad state of preservation, however, or if its epithelium has been macerated away, it then presents the appearance of a network of minute folds, a condition erroneously ascribed to the intact membrane. In the median part of the mid-gut, that which is

[1] *Proceedings Canad. Inst.*, Toronto, new series, vol. ii. No. 3.

directed forward, the crypts are as a rule smaller and less numerous, while the mucosa apparently is thinner.

In *Amia* the mucous membrane of the anterior section of the mid-gut shows a prominent network of folds, at the junction of every two of which occurs a prolongation outwards in the form of a villus. The surface is uneven, and the crypts visible to the naked eye seem to be but shallow cavities between the folds. As in *Acipenser*, the median portion possesses in its mucosa the characters of the anterior section, but in a less marked degree: its folds are smaller, its surface smoother, and its crypts less numerous.

In my preparations of *Lepidosteus* the mucous membrane is folded alike over the whole of the mid-gut, and presents insinkings of the epithelium to form structures analogous to the crypts in *Acipenser* and *Amia*.

In *Acipenser* the mucous membrane of the valvate section of the intestine is as thick as that of the anterior or duodenal section, but in the size and the number of the crypts it is like that of the median part. The crypts are all but absent from the surface of the spiral valve. In *Amia* the corresponding section of the mid-gut is in its anterior two-thirds lined with a mucosa of a character like that of the median portion which is directed forward. In the posterior third, containing the spiral valve, the mucosa of its wall, between the threads of the spiral, is provided with narrow longitudinal folds, oblique, or transverse ones being wanting. The larger crypts visible to the naked eye, occurring on the spiral valve, which is almost as smooth as in *Acipenser*, are very few in number and may be completely absent.

The number of turns in the spiral valve in *Acipenser* is usually eight, and the distance between them averages about 2·5 cm. The valve appears sometimes thin and membranous, at other times it is found to be very thick, the difference in size being no doubt due to the degree of distension to which the lymph- and blood-vessels are subjected. This portion of the intestine is always provided with a thick and unyielding muscular wall.

In *Amia* the spiral valve makes nearly four turns. It is not as thick nor as high as in *Acipenser*, and the turns of the spiral

are more closely approximated, being about three-fourths of a centimetre apart.

In *Lepidosteus* the valve makes three and a half turns, and in specimens of 7–10 cm. in length is so large as to fill completely the lumen of the intestinal tube. There is evidently a reduction in the number of turns of the spiral in advancing age, for, according to Balfour and Parker, in the fully adult specimen examined by them the valve does not complete the second turn.

A transverse section of the anterior portion of the mid-gut in *Acipenser* shows under the microscope a mucosa crowded with elongated crypts or tubules, each possessing a large lumen of varying diameter. They may open separately on the epithelial surface, or several may be united so as to open by a large common mouth. They are a continuation of those of the pylorus, but have acquired a differently constituted epithelium, which is, however, the same as that of the ordinary surface of the anterior part of the mid-gut. It is formed of one layer of cylinder cells, but there are at least two layers of nuclei observable (fig. 11). The nuclei of the lower layer are those of young cells destined to replace the cast-off or waste cells above them. The superficial cells have granular contents, often holding also fatty particles, and they possess a hyaline peripheral wall surmounted by a short fringe of cilia. The latter are to be observed only in carefully preserved material, and then they present very often the appearance of a coat of mucus on the ends of the cells. Goblet cells are not common.

In *Amia* a somewhat different appearance is presented by a transverse section of the anterior part of the mid-gut. Here the tubules densely crowding the mucosa are very much elongated, rarely branch, and radiate straight outward from the epithelial surface. These, as well as the epithelium, are constituted of short cylinder cells resting on four or five layers of nuclei. The cylinder cells are, apparently all of them, closed peripherally, and are fringed with strong cilia. It is impossible to trace in hardened preparations the outlines of the cells for more than a third of the depth of the epithelial stratum, the cause of this difficulty being the granulation and the extreme abundance of nuclei which are no doubt those of young cells.

The adenoid tissue of the mucosa is very scanty between the tubules, this being specially the case in *Amia*.

In *Lepidosteus* the tubules of the mid-gut are, in my preparations, but wide-mouthed pouches clothed with cylinder cells, having only one series of nuclei. The cells are longer and slenderer than in *Acipenser* and *Amia*, with delicate, often not detectable, cilia. Goblet cells are common; they occur very often in an exhausted condition; the body of the cylinder is more slender than usual, a small portion of the peripheral end remaining swollen and containing mucigen.

The histological relations of the median portion of the mid-gut in *Amia* and *Acipenser* are the same as those of the anterior portion. In the section containing the spiral valve in both genera, the epithelium is different in some respects, and the tubules fewer and shorter, while the adenoid tissue of the mucosa is more abundant. Goblet cells are more common, and the cylinder cells larger and more granular in their contents, the cilia also being longer and thicker.

In *Acipenser* the epithelium of the spiral valve is constituted, one-third at least, of goblet cells. The cylinder cells are very much elongated, and if observed in fresh condition they usually appear charged with fatty granules. Their peripheral ends are closed by a hyaline wall, covering which is a long brush of cilia[1] (fig. 13).

Many of these cells, when isolated carefully after maceration, show very fine processes which are sometimes dendritic at their terminations. The fact that the processes, more frequently appear to be divided than is the case with other epithelium of the alimentary tract, may be due to the greater ease with which they are isolated from the fibrous tissue of the mucosa, without injury or breakage. The outer halves of the goblet cells are much inflated. Their transformed contents are very granular, and project beyond the epithelial border in the form of a stopper.

In *Amia* and *Lepidosteus* the epithelium of the spiral valve does not differ from that of the neighbouring intestinal wall.

[1] According to F. E. Schulze these cells are provided with striated outer borders. It is possible that what was taken by this observer for a striation was in reality a fringe of cilia. I have been unable to find the original description by Schulze, and only saw a reference made by Edinger to it.

In *Acipenser* the tubules of the spiral valve are comparatively few in number and usually very short. The majority of them are but shallow insinkings of the epithelium, and in all of these goblet cells are very numerous. There are others, however, which differ somewhat from them, although a further study of fresh material may show both forms to completely resemble one another. Such tubules, of which but very few were seen, open into shallow pouches of the epithelium, and being much elongated they sometimes reach through half the thickness of the valve. They lack goblet cells. The fringe of cilia is much shorter and finer than that of the ordinary epithelium. Whether these structures are the representatives of the tubules in the anterior part of the mid-gut and in the neighbouring intestinal wall I do not know. They are probably derived from the latter, and if the present description of them is correct they form a class of structures which are unique in themselves, and in all likelihood perform the functions of the Lieberkühnian glands in higher vertebrates. In *Amia* I have not found similar structures on the spiral valve, the tubules and crypts of which are alike in every respect to those found on the ordinary intestinal wall.

In the axis of the spiral valve in *Acipenser* and *Amia* there is present a large quantity of unstriated muscular fibre, which in the last-named genus is aggregated into a single bundle. In *Acipenser* there are several bundles, arranged irregularly in direction and position. In vertical sections of the valve they sometimes appear separated by large lacunar spaces, which probably are the parts of lymph channels. At other times a muscular bundle appears almost surrounded by a closed follicle filled with leucocytes. In every case the bundles are distinctly marked off from the adenoid tissue of the mucosa. Scattered so irregularly as they are through the valve, it is almost impossible to conceive that they represent excessively developed portions of the *muscularis mucosæ*.

Lymph follicles are very abundant in the spiral valve of *Acipenser*, as many as seventeen having been counted in a single vertical section. They are usually round or oval in shape when near the epithelium, but of irregular form when nearer the centre of the valve, and always of varying size. When very numerous

the valve appears to be made up in bulk almost wholly of them. Sometimes they are placed so near to the epithelium that the latter appears to rest immediately on them. Around each follicle ordinarily the connective tissue is collected into a dense sheath, in which one can observe a number of corpuscles (fig. 14). The structure of the interior of the follicle can be made out only after the greater number of its cellular elements are removed, and this is accomplished by well agitating a thin section of the valve in water. Then, when stained, the close fibrillar network comes out clearly in the interior of the follicle, which still contains a few lymph corpuscles in the meshes of this network. At the same time, too, there can be seen in transverse section a large number of arterioles scattered over the field of the follicle.

Hyrtl [1] observed in the axis of the spiral valve in *Acipenser ruthenus* a large compact lymphoid organ, which he considered to be homologous with a similarly situated structure in *Lepidosiren*. Ayers [2] has found lymphoid capsules in the same species, and has given a figure of a vertical section of the valve to compare as to these capsules with one of the valve in *Lepidosiren*. They are undoubtedly homologous structures, although the anterior part of the organ in *Lepidosiren*, found outside the intestine, is lacking in *Acipenser*. A compact organ such as Hyrtl observed does not exist in *Acipenser rubicundus*, in which lymphoid follicles are more highly developed than in the species used by these authors for investigation.

Scattered collections of lymph corpuscles are very common in the various parts of the intestinal tract in fishes, and as such they simply represent an overloading of the adenoid tissue of the mucosa and submucosa with these structures, the limits of the deposit being rarely sharply definable. A compact lymph organ has been observed in the œsophagus of some Selachians, and, according to Edinger,[3] who has given the most detailed account of it, it possesses a capsule of connective tissue, from which trabeculæ of fibrils penetrating the interior divide and redivide,

[1] "Lepidosiren paradoxa," *Abhand. der böhm Gesell. der Wiss.*, 1845. I have had no opportunity for consulting this work, but found a quotation made by Ayers from it, which contains the view referred to.

[2] "Beiträge zur Anat. and Phys. der Dipnoër," *Jenaische Zeit.*, Bd. xviii.

[3] *Op. cit.*

cells similar to those of lymph being enclosed in the meshes thus formed. It would seem, from the descriptions of this and other authors, to be constant in presence and position, and it cannot therefore be one of those accidental infiltrations of the tissue with leucocytes which are so commonly found in every part of the intestine. It appears then that structures which may be correctly termed lymph follicles are to be found in the intestinal tracts of *Acipenser*, Dipnoi, and some Selachians only among fishes. Further research may, however, correct or extend this list.

In *Acipenser* the lymph follicles of the spiral valve are the representatives of the closed follicles forming the Peyer's patches in the higher vertebrates. They can usually be seen by the help of a magnifying hand-glass, as minute, whilst spots unequally distributed in the valve, which has, contrasted with them, a dull white colour. At some points they are so densely crowded together as to form an almost complete resemblance to a Peyer's patch.

The remaining part of the mucosa in the neighbourhood of the spiral valve in *Acipenser* and *Amia* is loaded with lymph corpuscles, although not nearly to the same extent as the follicles of the former.

End-Gut.

The relative lengths of this part of the intestine in *Acipenser* and *Amia* have been given above.

In some specimens of *Acipenser* there was practically no end-gut, the last turn of the spiral valve extending to the anal aperture. Where, however, it acquires any length, the mucosa covering it is either smooth or thrown into slender longitudinal folds, and is sometimes provided with minute crypts. The epithelium consists of cylinder and goblet cells, which gradually shorten to cubical cells, and at the vent to flattened cells, forming several layers in thickness. Anteriorly the cylinder cells bear a short fringe of cilia.

In *Amia* the inner surface of the end-gut is folded longitudinally; sometimes it is smooth and provided with crypts. When the epithelium is removed by maceration, the surface has a reticulated appearance. The epithelium consists of ciliated

cylinder cells with a few goblet cells. It undergoes a gradual decrease in height towards the vent.

In *Lepidosteus* the epithelium is of the character of that of the mid-gut, but the cilia are thicker and longer. At the vent the cells become cubical, which form gives no evidence of the possession of cilia.

I have observed in *Lepidosteus* the mesentery which connects the end-gut with the ventral wall of the peritoneal cavity, and which was discovered and described by Balfour and Parker.[1]

The Pyloric Appendage.

The pyloric appendage in *Acipenser* and *Lepidosteus* differs from similarly situated organs in other fishes, in that it is a compound structure with its pouches communicating with the intestinal cavity by a common duct, whereas in the great majority of fishes each pouch opens singly into the mid-gut. The latter arrangement is the primitive one; it can be seen in very young *Lepidostei*, in which the cæca arise as isolated outgrowths of the intestinal wall, and assume later a common duct, this being the manner of development in the Sturgeon also, according to Balfour.[2]

In *Acipenser* the organ is flattened on its inferior face, and appears uniform. The duct opens on the left side of the mid-gut, about a centimetre from the pyloric valve. It is of such a dimension in very large Sturgeons as to permit readily the introduction of the index finger into it for some distance, but in Sturgeon of ordinary size it is of the diameter of a goose-quill. Ten to twenty cæca, arranged in a radiate fashion, open into it at a distance of a centimetre or so from its intestinal aperture, all the cæca being enclosed in a common sheath of muscular and connective tissue. The mucosa of the duct and cæca is arranged in folds, crypts, and tubules, in much the same way as it is in the mid-gut. When denuded of its epithelium it appears possessed of the same characteristic network of the subepithelial tissues.

In a thin vertical section of the appendage, placed under the microscope, the structure of the mucosa is seen to differ un-

[1] *Op. cit.*

[2] *Comparative Embryology*, vol. ii. p. 632.

essentially from that of the mid-gut. The epithelium possesses more nuclear layers, the cilia are shorter, the cylinder cells slightly larger, and the goblet cells more extended than in the intestine. The connective tissue between the tubules is very abundant, and at various points in it there are collections of leucocytes.

The two muscular layers of the mid-gut are extended over the duct and cæca of the organ, but on the latter are arranged obliquely with regard to each other.

In *Lepidosteus* the organ appears more lobed, and presents the shape of a bean in young forms, in which it extends over the inferior face of the gall bladder and pancreas for some distance. Its lobes or cæca are very numerous, the common duct into which they lead opening into the mid-gut immediately behind the pyloric valve. The epithelial lining of both duct and cæca is of exactly the same character as that of the mid-gut.

In *Amia* there is no pyloric appendage.

Various theories have been put forward as to the function of these organs. The earliest opinion, and one for a time generally adopted, was that they act collectively as a pancreas in the absence of the latter organ. Whatever support this view had was taken from it when it was shown that pyloric cæca and a pancreas may consist in some fishes, notably *Lota*.

In 1860, Mordecai[1] advanced the view that these organs collect and store up fluid nutritious matter, which, during the passage of the fish to its spawning ground, is absorbed and utilised to repair the wasting processes of the body in the absence of ordinary food. His observations were made on *Alosa præstabilis* (*Clupea sapidissima*, Wilson), in which there are from sixty to one hundred separate cæca, and these, during the ascent of a river by the fish, were found distended with a brownish mucus, which was absent at other times of the year. Mordecai found also that the number of the cæca increase with age, and that in *Labrax* and *Dioplites*, some rudimentary in younger forms are functional in the fully adult.

According to Edinger,[2] the cæca serve to suck up the liquid

[1] His pamphlet is republished in the *Bull. U.S. Fish Commission*, 1881, p. 227.

[2] *Op. cit.*

and digested food matter as it escapes from the stomach, and absorb it. Wiedersheim[1] also adopts this view, and tries to show that the development of the pyloric appendages stands in inverse relation to that of the spiral valve. He mentions two instances of this: *Polypterus*, in which the pyloric appendage is but a short cæcal pouch, while the spiral valve is highly developed, and *Lepidosteus*, which has a well-developed pyloric appendage, but no spiral valve. This view of Wiedersheim, it must be said, cannot be held as generally correct, even when applied to the Ganoid fishes alone, for in *Acipenser*, in which the cæca being provided with a common duct is an evidence of the great development of these organs, there is a well-marked spiral valve, and in *Amia*, in which the spiral valve is almost as rudimentary as in *Lepidosteus*, there are no pyloric cæca.

Krukenberg[2] found in the cæca of *Acipenser sturio* evidence of the presence of diastase, pepsin, and trypsin. In other fishes these organs gave extracts containing one or more of the same enzymes. Krukenberg is, however, inclined to believe, after a long series of experiments, that the pyloric appendages perform specially the function of absorption.

According to Stirling's[3] view, these organs subserve different functions in different fishes, being absorptive in some, and in others glandular, secreting trypsin in some cases in important quantities.

Blanchard[4] found that the extract of the pyloric cæca in various fishes effects the transformation of boiled starch into grape sugar, and that when boiled white of egg or fibrin is added to the extract, whether this is alkaline, acid, or neutral in its reaction, peptones are formed. He believes that a tryptic ferment alone is present to accomplish the latter result.

During the summer of last year, I made a number of experiments with extracts of the pyloric organ in *Acipenser*, in order to determine the presence of the enzymes, which Krukenberg affirms he found there. For this purpose large fish were employed. The organ after its removal was slit open, the mucous matter in the duct and cæca quickly washed away, to

[1] *Lehrbuch der Vergl. Anat.*, p. 565.
[2] Kühne's *Untersuchungen*, Bd. ii., 1882.
[3] *Journal of Anat.* and *Phys.*, vol. xviii. p. 426.
[4] *Comptes rendus*, xcvi. 1241–1244.

remove such enzymes as might have gained entrance from the intestine, and which would vitiate the result. It was then in some cases finely minced, and in this condition covered with distilled water in a flask surrounded by ice for twenty-four hours; in others it was carefully dried, and in a finely divided state extracted at a temperature of 35° C., with a 0·2 per cent. solution of hydrochloric acid, or with a 0·5 per cent. solution of sodic carbonate. With extracts made with distilled water, no conversion of starch into grape sugar could be obtained, and in no case could the presence of the latter substance be detected. Almost always an emulsion occurred when a quantity of the extract was shaken with some olive oil and allowed to stand. From the acid or alkaline extracts of the finely divided organ I was unable to obtain the slightest traces of digestion when fibrin or boiled white of egg was treated with them; if, however, the organ was slightly sponged, instead of being quickly washed with water, traces of pepsin and trypsin were found, but no diastase, although grape sugar could be detected in very slight quantities. The presence of trypsin can be easily explained in this case, as the opening of the pancreatic duct is just opposite that of the pyloric organ, and in the first contraction of the intestine after the pancreatic fluid escapes some of the fluid must find its way into the duct and cæca, even if it does not reach them by any other means, *e.g.*, diffusion. The pepsin gains access in like manner from the fluid contents of the stomach, immediately after passing through the pyloric orifice.

The difference between the results obtained by Krukenberg and those here detailed, as to the presence of enzymes in the pyloric appendage of *Acipenser*, may be accounted for on the ground that in all the material used by me the stomach and intestine were completely empty, while it is barely possible that it may have been otherwise with that employed by Krukenberg, since enzymes are more likely to be present in detectable quantities when food matter is in the intestinal canal.

Although it is an important matter to establish whether the enzymes referred to are present or not in the pyloric cæca, and in what quantities, yet such an accomplishment must not be allowed to decide definitely what the function of the organs is in the great majority of fishes. Pepsin and trypsin may be

normally present as a result of their easy diffusion, as is sometimes observed in organs not immediately connected with the alimentary canal in higher vertebrates, or they may be present as the result of the active secretion of the cæca. That such a secretion can occur and does, is possible, apart from the fact that in certain fishes, *e.g.*, in the cod, according to Stirling, the cæca are provided with gland structures of the usual form. It is true that the cæca are lined with cylinder cells usually, to which there has not yet been attributed the power of secreting either pepsin or trypsin. But when it is seen that the long cylinder cells lining the intestinal tract and the so-called liver in *Amphioxus* must secrete whatever enzymes are used in the digestion of the food swallowed, one is compelled to ask, Why should not a somewhat similar epithelium in the pyloric cæca of fishes perform a like function? The secretory function of this epithelium, as Stirling points out, does not exclude that of absorption, this also being exemplified in the case of *Amphioxus*. We see, therefore, that it is not easy to determine definitely the function of these organs in all fishes; in some, absorption may overshadow secretion, in others, the reverse may occur, while in others again, the two functions may occur in equal proportions. This would explain the contradictory results obtained by different observers in this field of research.

In any case, it is fair to conclude that the pyloric cæca are rudimentary structures once actively glandular. They are in their development remarkably similar to other outgrowths of the intestinal wall in their immediate neighbourhood, *i.e.*, the liver and pancreas. It seems extremely probable that at one time in the history of vertebrates there opened into the alimentary canal, which had a simpler form than it now possesses, a large number of pouch-like diverticula, and that by gradual specialisation of some of these arose posteriorly the liver and pancreas, anteriorly the air bladder, and, if they are not homologous with the latter, the lungs, while others retained their primitive structure and arrangement, persisting as pyloric cæca. In consequence of this specialisation, all the functions, such as those of absorption and of the secretion of enzymes, possessed by the original cæca, would necessarily be retained in an impaired degree by those persisting in that form.

It is to be expected, also, that the digesting principles secreted by the cæca partake more or less of the characters of those of the primitive organs. We may in this way explain the occurrence of such an enzyme as Blanchard found in the pyloric appendages, which digests in an alkaline, acid, or neutral solution; this, probably, was the character of the primitive seeretion, not only of these organs, but of the whole intestinal tract, and by a course of selection operating in the organs and their functions the secretion came in the course of time to present in the stomach the properties of pepsin, in the pancreas those of trypsin. We have then a clue to an explanation of the supposed presence of both enzymes in the pyloric cæca; one enzyme in reality is present, which digests fibrin in an alkaline or an acid solution, and which partakes of the characters of both pepsin and trypsin.

The Pancreas.

It is over half a century since the first observation on the pancreas of fishes was published, and it is only twelve years ago that the presence of such an organ was demonstrated to be general in this class. To Legouis belongs the honour of having accomplished the latter task.

This observer[1] has given a full history of the researches of the various anatomists on the subject, and on this account further reference to the general literature bearing on it may be avoided. With regard, however, to that treating of the pancreas of Ganoid fishes a few words here are necessary.

In 1833 Alessandrini[2] discovered a pancreas in the Sturgeon. After a number of anatomists had failed to confirm this discovery, Leydig[3] recognised the accuracy of Alessandrini's description, and, what the latter had not done, gave a short account of the histological structure of the organ.

Alessandrini's and Leydig's statements have not been confirmed by the researches of a third observer up to the present date. Wiedersheim[4] describes as the pancreas an organ extending from

[1] *Ann. des Sciences Nat.*, 1873.

[2] *Ann. des Sciences Nat.*, t. xxix., 1833; also *Acad. Scien. Inst.*, Bonon, 1835, tom. ii.

[3] *Untersuch. über Fische und Reptilen*, Berlin, 1853.

[4] *Lehrbuch der Vergleich. Anat.*, p. 605.

the pyloric appendage down the left side of the anterior portion of the mid-gut, while Krukenberg[1] found no organ specially performing the function of a pancreas, and he maintains that the organ of Wiedersheim, which he regards as the spleen, is neutral as to digestion, its extracts having no action whatsoever. Ayers[2] has given a figure of a section of the supposed pancreas, and he recognises it as constituted of lymphoid tissue.

No reference has hitherto been made in the literature to the occurrence of a pancreas in *Amia*.

In *Lepidosteus* Balfour and Parker[3] found a pancreas in young forms, it being situated, according to their description, behind the liver in the loop of the pyloric section of the stomach. They found also that it arises in the embryo in the same manner as in other vertebrates, and that late in larval life it envelops the anterior section of the bile-duct. In the fully adult *Lepidosteus* they observed a small, apparently glandular, mass connected with the bile-duct, and occupying a position similar to that of the pancreas in the larva. They were unable to decide on its nature, as its poor preservation did not permit a histological examination.

In *Acipenser*, the organ considered by Wiedersheim to be the pancreas is really the spleen, as a careful study of its histology will show.

The true pancreas in this fish is a disseminated one, *i.e.*, its tissue is not localised, but variously extended throughout the the right half of the peritoneal cavity. It occupies on the whole the position described by Alessandrini and Leydig. Its tubules and ductlets entwine about the branches of a blood-vessel (*arteria cœliaco-mesenterica*), which it accompanies down the valvate portion of the intestine, on the median and anterior portions, and into the liver (fig. 16). It was in sections of the last-named organ that I found it first. It is more disseminated in some specimens of *Acipenser* than in others; for example, in one I found that it extended 8 cm. down the length of the valvate portion of the mid-gut, while usually the distance extended is only about 3 cm. The greater bulk of the organ is found

[1] Kühne's *Untersuchungen*, Bd. i. and ii.

[2] *Jenaische Zeitschrift.*, Bd. xviii. p. 479, taf. xvii. fig. 52.

[3] *Phil. Trans.*, 1882, pt. i. p. 359.

between the liver and the second bend of the mid-gut on the right side, and is easily detectable from the thickness of the walls of the blood-vessel referred to, consequent on the pancreatic tissue enveloping them. As a branch of this artery enters the accessory spleen (fig. 16, *asp*), vertical sections of the latter organ sometimes betray the presence of the pancreatic tubules.

The serosa covering the pancreatic tissue and the vessels has usually a dark colour, sometimes perfectly black, owing to the presence of a large number of pigment cells.

The portions of the pancreas which are attached to the intestinal walls are always closely applied to the latter and included within the serosa.

The pancreatic duct opens into the mid-gut on the dorsal side; its aperture and that of the bile duct being found on a prominent papilla on the inner intestinal surface, not more than half a centimetre usually from the tip of the pyloric valve. I have never succeeded in injecting the pancreatic duct with coloured fluids so as to show its course. It is easily distinguishable from the bile duct by the greenish tinge which the latter always has.

In *Acipenser sturio* Alessandrini found the bile duct and the pancreatic duct to open on separate but similar papillæ on the inner wall of the mid-gut, that on which the opening of the pancreatic duct is found being placed more than 2 cm. from the pyloric valve. I cannot find this to be the case in *Acipenser rubicundus*, in which, by snipping off the point of the single papillæ above referred to and spraying the stump with water, one can easily see the two apertures placed side by side on it.

In *Amia* the pancreas is disseminated in a manner similar to what it is in *Acipenser*. A part of it is found adherent to the extreme anterior end of the mid-gut (fig. 10, *pn*); but a greater part envelops the larger branches of the portal vein in the interior of the liver. It forms a large portion of the bridge between the right and left hepatic lobes, and it covers, to a certain extent, the arch of the bile duct.

The pancreatic duct is here also hard to trace. I did this, however, in a young *Amia* of about 6 cm. in length, by means of a series of vertical sections made by Professor Ramsay Wright, who was the first to observe the presence of a pancreas in this fish. A careful dissection of the tissues about the bile duct in

the adult gave the same result as the study of the series of sections. The pancreatic duct is much narrower in diameter than the bile duct, to which it is nearly parallel, and near the intestinal wall they both have a common investment of connective tissue, the one thereby appearing to open into the other. They remain completely separate, and their apertures are to be found on the apex of a slender papilla placed about 1·5 cm. from the pyloric valve. The course of the two ducts is from before backward, almost in a line with the anterior part of the mid-gut.

In *Lepidosteus* the pancreas is not so widely disseminated as in either *Acipenser* or *Amia*. It envelops the portal vein as it runs along partially sunken in the dorsal face of the liver, in the posterior third of this organ, while it reaches behind accompanying the same vein to a point opposite the posterior extremity of the pyloric appendage (fig. 1, *P*). Some of its tubules are adjacent to the superior face of the gall bladder, others twining about the bile duct for some distance. In the liver the tubules radiate frequently out from the vicinity of the portal vein between the hepatic lobules. Both the bile duct and that of the pancreas run side by side backward to the mid-gut, the pancreatic duct being placed on the gastric side of the other. Adjacent to the wall of the mid-gut the two ducts become fused. In a transverse section of this part of the body it is possible to distinguish this common duct from a pyloric cæcum only by tracing it from behind forwards, since the histological structure of both near their termination in the intestine are alike in every particular. Opposite the pyloric appendage, and above the pylorus, is a small quantity of lymphoid tissue, which, though it contains a few tubules of the pancreas, is not the latter organ, as Balfour and Parker suppose. This, usually as large in vertical section as the mid-gut, and, traversed by the portal vein, seems to be an accessory spleen, the pancreatic tissue forming but a very small part of it.

I have not had an opportunity of studying sections of the liver of an adult *Lepidosteus*, but I have no hesitation in saying that such sections, if taken through the posterior third of the organ, would show well-developed pancreatic tissue surrounding some of the larger vascular channels near the dorsal surface, and

that the pancreas in this fish is not inferior, structurally and functionally, to what it is in either *Acipenser* or *Amia*.

With regard to the finer histology of the pancreas in the three genera a short description only can be given here, as the quantity of material at my disposal did not allow very varied methods of preparation.

In *Acipenser* the structure is very much as in the higher vertebrates. In the necks of the tubules, which may also be termed the intermediary canals of the alveoli, the lining epithelium is constituted of cubical cells. In the alveolar portions the cells are large, the nuclei distinct and arranged in the peripheral halves of the cells, while the central halves are filled with granules. In my preparations the nucleus may be said to be the only part of the cell which stains in carmine or hematoxylin, as it is rare that the protoplasm in the immediate vicinity of the nucleus takes any tint at all. The alveolar lumen is usually distinct and of a zigzag course. Transverse sections of the tubule in its various parts exhibit the usual characteristic appearances.

Among the cells and in the lumen of each alveolus, there are other cellular elements, which are noticeable at first sight on account of the deep and nearly uniform staining which they take, and also on account of their varied shape, sometimes oval or polyhedral, and sometimes amœboid. Granules are lacking, the protoplasm appears clear, and no reticulation was observable in it. The nuclei always stain much more deeply than those of the ordinary cells of the alveoli. The cells are oftenest to be found in the lumen, and then they appear sometimes to send out processes between the gland cells (fig. 17, C.). They are, I think, remarkably similar to the centro-acinar cells of Langerhans. I have never met with these structures in any other fish.

The arrangement of the tubules about a branch of the *arteria cœliaco-mesenterica* is indicated in fig. 17, A. Trabeculæ of connective tissue radiate outward between the tubules to the serosa, the latter possessing a large number of pigment cells, to which the dark colour commonly associated with the pancreas in this fish is due.

In *Amia* the pancreatic tubules imbedded in the liver are twined about the larger branches of the interlobular veins in the

manner represented in fig. 18. The connective tissue of the interlobular septa run between and separate the neighbouring tubules, which in a vertical section of the liver appear cut in various directions, oftener longitudinally. The cells of the aveoli are, in their central portions at least, crowded with granules, and stain very feebly apart from their nuclei. Near the lumen the limits of the cells are indistinct, owing to the quantity of granules present. The lumen sometimes is, and sometimes is not, visible.

In *Lepidosteus* an alveolar and an intermediary portion can be distinguished in each pancreatic tubule.

The pancreas would appear to be rudimentary or absent in but very few fishes. There are conditions when such an organ seems to be useless, and these are found in small fishes only, such as some of the Cyprinoids, in which digestion by the stomach alone prepares enough of nutritious material for absorption to satisfy the demands of the organism, and in which the mid-gut does not serve to submit the food matters escaping from the gastric cavity to a second digestive process but to a further absorption. No such reason can be advanced for the supposed absence of the pancreas in large fishes. Its presence is so disguised in many forms that one finds it impossible to decide definitely whether it is absent in others. In Ganoids, as above described, it is partially imbedded in the liver, in some Siluroids [1] completely so. Why may it not be connected in a like manner with the liver in other forms in which it is now supposed to be absent? That this is frequently the case is probable from the occurrence of trypsin in the extracts of the liver of various fishes, as shown by Krukenberg. The liver and pancreas thus fused into one organ can of course in no case be considered as a hepato-pancreas.

[1] In *Amiurus* the pancreas is imbedded in the interior of the liver, its tubules being entwined about the interlobular veins, (see *Proceedings Canad. Inst.*, Toronto, new series, vol. ii. No. 3).

EXPLANATION OF PLATE XX.

Fig 1. The alimentary canal and pancreas of *Lepidosteus*, from a specimen measuring 10 cm. *a*, œsophagus; *b*, the commencement of the stomach anteriorly; *c*, the pylorus; *e*, the anterior or duodenal section of the mid-gut; *f*, the posterior, or valvate, section of the same; *at*, the hind-gut; *ap*, the pyloric appendage; *p*, the pancreas. (Reduced.)

Fig. 2. A longitudinal section of one of the papillæ of the so-called œsophagus in *Acipenser*.

Fig. 3. An oblique section of a dilated sac from the œsophagus of *Acipenser*.

Fig. 4. A transverse section of a dilated sac from the œsophagus of *Amia*.

Fig. 5. A tubule from the mouth of the air-duct in *Amia*.

Fig. 6. A vertical section of a fold of the mucosa of the œsophagus of *Lepidosteus*, showing ciliated epithelium and dilated sacs.

Fig. 7. Two glands from near the posterior part of the cardia in *Acipenser*.

Fig. 8. A gland from the cardia of *Amia*. *a*, one seen in transverse view.

Fig. 9. Part of a mucous gland from the pylorus of *Acipenser*.

Fig. 10. A vertical section of the wall of the anterior part of the mid-gut in *Amia*. *pn*, the pancreas; *m*, the mucosa; *i*, the inner, *o*, the outer, muscular layer.

Fig. 11. Epithelium of a crypt of the mid-gut in *Acipenser*.

Fig. 12. Part of a vertical section of the spiral valve in *Acipenser*, showing the short pouches of the epithelium, and the mucosa underneath richly laden with lymph corpuscles.

Fig 13. Epithelium of the same section more highly magnified. *a*, a young epithelial cell.

Fig. 14. A section of a lymph follicle from the spiral valve of *Acipenser;* the greater number of lymph corpuscles have been removed from the section by agitating it in water.

Fig. 15. Epithelium of a tubule of the spiral valve of *Amia*.

Fig. 16. A view of the mid-gut and the organs attached to it in *Acipenser*. *Ap*, the pyloric appendage; *sp*, the spleen; *a.sp*, the accessory spleen; *p*, the main portion of the pancreas surrounding a branch of the *arteria cœliaco-mesenterica; p'*, *p''*, pancreatic tissue adhering to the smaller branches of this vessel, and to the wall of the mid-gut; *l*, the liver, the course of the pancreatic tissue in which is represented by dotted lines; *m*, the anterior portion of the mid-gut; *v*, the valvate portion of the same.

Fig. 17. *A*, A section of a branch of the *A. cœliaco-mesenterica* in *Acipenser*, with pancreatic tubules surrounding it, a portion only of these being represented; *B*, a part of one of the tubules more highly magnified; *C*, a transverse view of one of the tubules. In both *B* and *C* the centro-acinar cells have a darker shading. *B* and *C* highly magnified.

Fig. 18. From a vertical section of the liver in *Amia*, showing the manner in which the pancreatic tubules are arranged around a larger interlobular vein; *pt'*, one of the tubules seen in transverse section; *vt*, an interlobular vein filled with blood-corpuscles.

Fig. 19. From a vertical section of the dorsal face of the posterior part of the liver in *Lepidosteus*, showing the arrangement of the pancreatic tubules *pt* about the portal vein (*vp*); *h*, liver tissue; *b*, the bile duct.